

RELATIONSHIPS AMONG SONG ACTIVITY, CONTEXT, AND SOCIAL BEHAVIOR IN THE WARBLING VIREO

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The songs of most passerines are classic examples of a nested hierarchical structure. They can be described at a number of levels where each level is made of components and their relationships, which together form the next higher level (see Simon 1962, Polanyi 1968, Mesarovic and Macko 1969, Dawkins 1976). Examples of levels in song are figures, phrases, songs, bouts, circadian cycles, seasonal cycles, etc. The studies of avian communication that are concerned with the encoding of information and its relationship with context have focussed mainly on changes in structures at the level of song or below (for examples see Marler 1956; Falls 1963, 1969; Smith 1965, 1968, 1977; Morse 1967; Emlen 1972; Armstrong 1973; Catchpole 1973; Kroodsmma 1975, 1977; Lein 1978; Smith et al. 1978). Most of the studies on levels above that of song relate changes in song activity to changes in the components that make up song (for examples see Hinde 1958, Thompson 1972, Armstrong 1973, Heckenlively 1976). Numerous factors have been described which influence the amount and rate of singing (Thorpe 1961, Armstrong 1973, Slagsvold 1977). Although certain relationships between changes in song activity with season and context are well known (e.g., mate attraction, territorial behavior, courtship, relationship to the breeding cycle), studies tend to be anecdotal and suffer from a lack of quantitative data (Catchpole 1982). If song is taken as the unit of analysis, do differences in the temporal patterning of song encode different messages, and if so what significance do these changes have on social behavior?

In this study the song activity of the Warbling Vireo (*Vireo gilvus*) in southern Ontario is examined. The purpose is to describe and quantify relationships among cadence, song rate, breeding cycle, and context, and to determine their possible importance in the social behavior of the pair.

METHODS

Warbling Vireos were studied in Cootes Paradise Sanctuary, Royal Botanical Gardens, Hamilton, Wentworth Co., Ontario, from May to August in the years 1975-1977. Vireos were observed in the same time interval each day. During each observation period an attempt was made to record all songs given by the same individual for periods ranging from 20 to 60 min duration. The same birds were followed each day during the season. Song activity was documented on data sheets marked out in minutes and seconds. When nest-building began, an observer remained near the nest and recorded behavior in detail while another

observer followed the male. Since males sang fairly constantly for most of the nesting cycle, their activities could be observed in detail. Birds were not marked, however, individuals could be distinguished in most circumstances based on characteristics of song, behavior, and use of song perches. No male replacements were suspected based on changes in the above characters and in male-female interaction. Males occupying isolated territories were selected to aid observation. Song data presented in this study were gathered on two males in 1975, eight males in 1976, and four males in 1977. One male each in 1975 and 1976 and three males each in 1976 and 1977 occupied similar territories.

I categorized song activity into six contexts based on the proximity of a bird to its mate and nest. I selected the distance of 10 m as the point beyond which a bird was considered distant from the nest or alone (i.e., from its mate) based on observations which I had previously made in 1975 on defence and vocal behavior. The term 'alone' refers to situations where the male is not in the company of its mate.

Contexts include: (1) Male-pre-pair—male is unmated and on territory. (2) Male-alone-distant—male is mated, more than 10 m from the nest, and is alone (includes situations in which the male is alone prior to nest construction). In this context the male either is patrolling the territory or is foraging. (3) Male-alone-near-the-nest—male is within 10 m of the nest and alone. (4) Male-on-the-nest—male is sitting on the nest (i.e., incubating or brooding); female may also be nearby. (5) Male-female-near-the-nest—mates are within 10 m of each other and the nest; female may be sitting on the nest. (6) Male-female-distant—mates together and more than 10 m from the nest; includes situations in which the pair is together prior to nest-building.

These contexts facilitated examination of the possible effects of the proximity of the nest and female on the singing behavior of the male. Interactions between neighbors were not investigated. A male may be influenced by a neighbor's song anywhere in his territory. To reduce effects of neighbor interaction on male song, I did not further consider song given by a territory holder in encounters involving chasing or intense vocal duelling with a neighbor.

Under the term 'song activity' are described the following four variables. 'Cadence' is the interval in sec between the start of consecutive songs (Reynard 1963). In frequency distributions of cadence, frequency values decreased rapidly at a cadence of about 20 sec. Therefore, I examined cadence up to an arbitrarily selected limit of 30 sec. In the text the term 'singing rate' excludes 0 songs/min in its calculation, whereas, 'song rate' includes 0 songs/min in its calculation. 'Time spent silent' is the number of minutes in a sample with 0 songs/min.

Song output refers to the quantity of song. A 'song bout' is defined as a group of songs or a song separated by an interval equal to or less than 59 sec, and a 'song bout interval' as an interval of 60 sec or more between songs (Thompson 1972). Courtship calls are given by females. The contextual relationships of these calls are complex, however, most are associated with courtship activity and function as a precopulatory solicitation signal (Howes-Jones 1982). A preliminary analysis of song data showed that contextual differences in song activity remained independent of changes in the breeding cycle. I, therefore, lumped data on context for the breeding cycle (Table 1).

RESULTS

Description of song.—The song of the Warbling Vireo is complex and highly variable in structure. Song duration averages about 2.5 sec. The figures that make up song are about 0.1 sec in duration and are separated by intervals of about 0.03 sec. Figures are variable in shape, as are patterns

TABLE 1
MEAN AND STANDARD ERROR FOR CADENCE, SINGING SONG RATE, SONG RATE AND TIME SPENT SILENT FOR WARBLING VIREOS IN DIFFERENT CONTEXTS

	Context					
	Male-pre-pair (3) ^{a,b}	Male-alone-distant (10)	Male-alone-near-nest (10)	Male-female-near-nest (10)	Male-on-nest (10)	Male-female-distant (10)
Cadence (sec)	9.60 ± 0.84	9.38 ± 0.23	9.56 ± 0.26	9.46 ± 0.27	14.03 ± 0.68	13.19 ± 0.34
Range	7.6-10.9	8.5-10.8	8.2-11.1	8.1-10.8	10.7-18.0	11.8-15.4
Singing rate (excludes 0 songs/min)	4.89 ± 0.66	5.07 ± 0.14	5.08 ± 0.24	5.20 ± 0.27	3.27 ± 0.31	2.71 ± 0.14
Range	4.2-6.2	4.4-5.8	4.1-6.4	4.2-6.8	1.9-4.8	2.1-3.3
Song rate (includes 0 songs/min)	4.00 ± 0.52	3.03 ± 0.25	4.75 ± 0.20	4.88 ± 0.31	2.40 ± 0.35	1.26 ± 0.19
Range	3.2-5.3	1.9-4.3	3.9-5.8	3.4-6.5	0.4-4.5	0.4-2.1
Time spent silent (%)	18.6 ± 2.1	39.8 ± 4.3	6.6 ± 1.3	7.1 ± 1.8	30.1 ± 5.9	55.1 ± 5.1
Range	15.1-23.5	18.7-59.1	0-14.6	1.0-21.2	5.3-78.6	31.8-77.2

^a Number of individuals.

^b Sample sizes for individuals varied between 52 and 913 for cadence, 24-357 min for song rates, and 24-941 min for time spent silent.

formed by groups of figures. The structure of song and its changes with respect to song activity and context are complex and will not be discussed here (Howes-Jones 1982, unpubl.).

Changes related to context and proximity.—Table 1 summarizes variations in song activity with context. Analysis of variance indicated there were significant differences in cadence, singing rate, and overall song rate among contexts ($F = 20.81, 20.63, 23.47$, respectively; $P < 0.01$). The sum of squares simultaneous test procedure (Sokal and Rohlf 1969) was used to test for differences among contexts.

In general, song activity in the contexts male-alone-near-the-nest, male-female-near-the-nest, male-alone-distant, and male-pre-pair were similar. There were no significant differences ($P > 0.05$) in the above contexts with respect to cadence or singing rate. The frequency distributions for each of the contexts resembled each other for cadence and for singing rate (see distribution for male-near-the-nest in Figs. 1, 2). Among individuals, the most frequent modal values for cadence was 7 and 8 sec (23 of 33 times) and for singing rate between five and seven songs/min (24 of 33 times).

The only difference in song activity among the four contexts was in the continuity of output that became evident when overall song rates were compared. Highest song rates occurred in the contexts male-female-near-the-nest, male-alone-near-the-nest, and male-pre-pair. No significant differences were found ($P > 0.05$). Mean song rate for the context male-alone-distant was significantly lower than the above three contexts ($P < 0.01$). The difference was due to the amount of time birds were silent in each context. When males were near the nest they sang almost continuously (93% or greater), whether they were with the female or not. Unmated males also spent most of their time (81%) singing. By comparison, in the context male-alone-distant males were silent about 40% of the time.

The longest cadences and lowest song rates were recorded in the contexts male-female-distant and male-on-the-nest (Table 1; Figs. 1, 2). For both contexts the mean cadence, singing and overall song rates were not significantly different ($P > 0.05$), but the two contexts were significantly different from the other contexts for all three variables. The difference in cadence between the two groups was approximately 4 sec. Song given on the nest has a regular cadence (Fig. 3C). Songs given in the context male-female-distant tend to be given sporadically (Fig. 3A). In 7 of 10 individuals, the variance in cadence was significantly greater ($P < 0.05$, F -max test) in the context male-female-distant than in the context male-on-the-nest. The average coefficient of variation (c.v.) for male-on-the-nest was lowest among contexts, (38.8, $N = 10$) whereas, the c.v. for the former context was highest (48.8, $N = 10$). In the context male-female-distant,

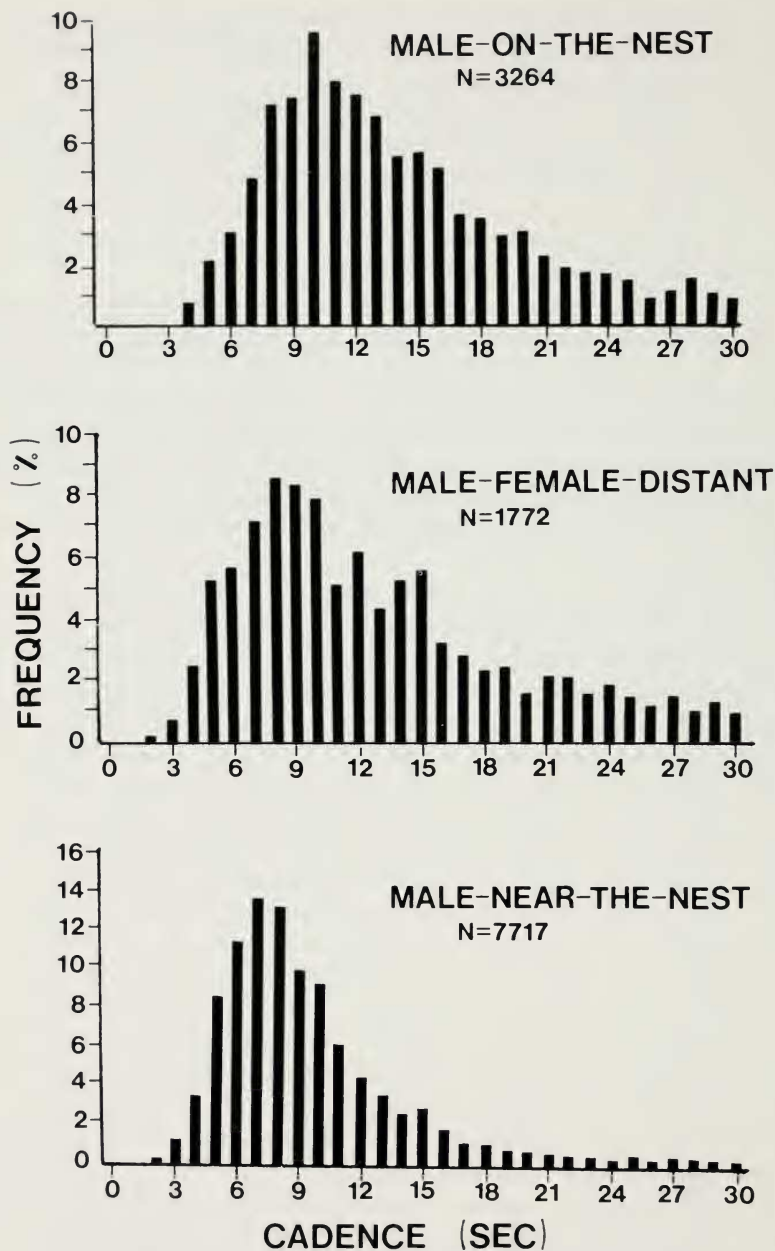


FIG. 1. Frequency distributions of cadence among contexts for 10 males. The context male-near-the-nest includes the contexts male-alone-near-nest and male-female-near-nest.

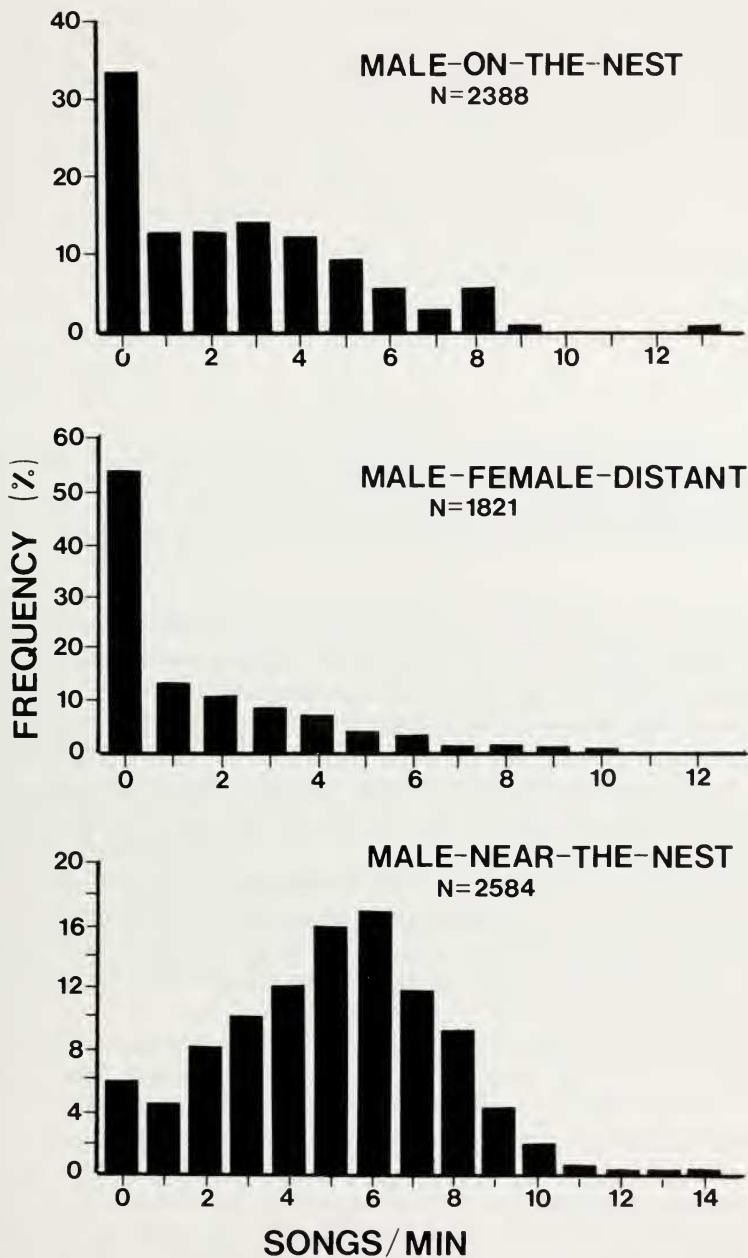


FIG. 2. Frequency distributions of song rate among contexts for 10 males. Male-near-the-nest is the same as in Fig. 1.

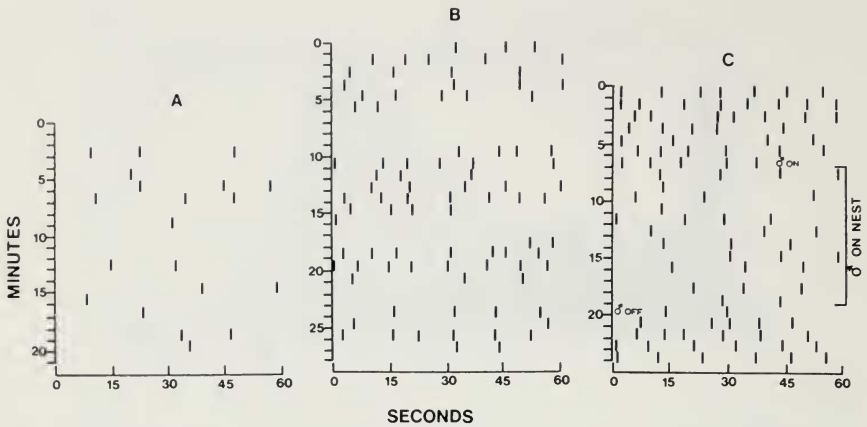


FIG. 3. Examples of song records from the field to demonstrate typical differences in the temporal patterning of song with context. Each mark denotes a song. Patterns were taken from different males. (A) Male-female-distant. (B) Male-alone-distant. (C) Between the 7th and 20th min the male is on the nest; during the rest of the time the male is near the nest.

males were silent most of the time (55.1%) (Fig. 2). Males tend to sing continuously while on the nest and only fall silent toward the end of the incubation period or at the start of the nestling period.

The stimulatory influence of song from neighboring males is indicated by the small modal value for cadence in the context male-female-distant in Fig. 1. If a neighboring male is singing nearby, then the resident will engage in a song duel whether the female is present or not. The result is an increase in the number of cadences of short duration in the sample. However, all such effects could not be eliminated. It was obvious from field observations that male song activity decreased substantially or ceased in the following circumstance—when the male and female were together and not near the nest and when there were no other males singing nearby (see Fig. 3A).

Abandoned nests or mates.—In one pair the female disappeared late in the incubation period. Song output increased significantly (approx. $t = 8.585$, $P < 0.05$) from the 3 days prior to the disappearance (1.93 songs/min, $N = 126$ min) to the 3 days after (5.41 songs/min, $N = 113$).

The nests of two pairs were destroyed late in the incubation period; renesting did not take place. In both instances song output did not significantly change from the 3 days prior to nest destruction (2.35 songs/min, $N = 133$; 2.25 songs/min, $N = 118$) to the 3 days after (2.56 songs/min, $N = 111$; 2.03 songs/min, $N = 120$).

Bout structure.—There did not appear to be any consistent pattern in the delivery of song (i.e., bouts) among contexts. In male-pre-pair and male-alone-distant, birds tended to sing in bouts followed by intervals of silence of varying length (Fig. 3B). When near or on the nest, males sang almost continuously (Fig. 3C). In the context male-female-distant no obvious bouts were apparent (Fig. 3A).

Data on the bout structure of one male were gathered from all contexts and for the entire season. The mean number of songs per bout was 25.5 ($N = 149$ bouts), the mean bout length was 5.2 min ($N = 148$ bouts), and the mean interbout interval was 5.0 min ($N = 134$ intervals). The mean cycle length (the time from the beginning of one bout to the beginning of the next) was 10.2 min.

Changes related to the breeding season.—The song output (all contexts) of Warbling Vireos during the nest cycle is summarized in Table 2. Periods have been subdivided to show the changes in song output which occurred at the transition between periods. Durations of subdivisions were arbitrarily chosen or, in the case of shorter intervals, were chosen to increase individual sample size.

Most variation in song output during the season can be ascribed to two factors. The first relates to changes in context and the second to long term, likely physiological, changes. Since song activity changes with context, changes in song output during the season may reflect the time spent by birds in various activities. If a bird's physiology changes during the season, then it may be assumed that song output, irrespective of context, would also be affected to some degree. To help determine if this was occurring, song output was tabulated from one context (male-alone-distant) for the entire season (Table 2).

There was no significant difference ($t = 1.869$, $P < 0.10$) in overall song output from the pre-pair to the pre-nest-building period. In the pre-nest-building period mates spend on average 80.4% ($N = 1245$ min, $N = 7$ pairs) of their time together (within 10 m of each other). In this context male song activity was low (Table 1). Therefore, overall song output for the period would also be expected to decrease. It has often been reported in passerines that song activity of unmated males decreases substantially upon arrival of a mate (for reviews see Armstrong 1973, Catchpole 1982). However, it has not often been specified whether the effect is general or context dependent. The song rate recorded in the pre-pair period (male-alone-pre-pair, Table 2) was only slightly lower than the song rate of the comparable activity (i.e., patrolling the territory) in the pre-nest-building period (male-alone-distant, Table 2). The song rate was also calculated when the male was with the female during the pre-nest-building period

TABLE 2
 MEAN SONG RATE AND STANDARD ERROR DURING THE BREEDING SEASON FOR ALL
 CONTEXTS AND FOR MALE-ALONE-DISTANT

Period	Sample interval (days)	Songs/min all contexts N ^a $\bar{x} \pm SE$ range \bar{x}^b	Sample interval	Songs/min male- alone-distant N $\bar{x} \pm SE$ range \bar{x}
Pre-pair	entire	4 (49-101) 3.10 \pm 0.76 0.99-5.27	entire	—
Pre-nest-building	up to last 3 days	8 (26-325) 1.84 \pm 0.30 0.33-3.10	entire	7 (34-66) 4.00 \pm 0.28 3.11-4.94
	last 3 days	9 (63-118) 2.04 \pm 0.41 0.19-4.66		
Nest-building	first 2 days	11 (60-245) 2.98 \pm 0.23 1.70-4.24	first half	9 (23-120) 3.69 \pm 0.30 2.01-5.30
	middle	12 (34-156) 2.90 \pm 0.33 1.74-5.56	second half	10 (28-82) 4.62 \pm 0.47 2.88-7.32
	last 2 days	12 (60-154) 2.78 \pm 0.35 1.24-5.46		
Incubation	first 3 days	12 (100-265) 4.10 \pm 0.52 1.42-7.03	first 3 days	8 (23-95) 5.33 \pm 0.64 2.28-8.54
	middle	13 (206-641) 3.19 \pm 0.34 1.31-6.02	middle	8 (69-242) 3.78 \pm 0.24 1.49-6.26
	last 3 days	11 (66-180) 2.68 \pm 0.32 0.98-4.71	last 3 days	9 (17-99) 2.95 \pm 0.34 1.59-4.04
Nestling	first 3 days	11 (88-180) 1.99 \pm 0.30 0.36-3.67	first 3 days	9 (13-88) 2.41 \pm 0.40 0.38-4.11
	middle	11 (100-440) 2.31 \pm 0.32 0.67-3.94	middle	9 (44-217) 2.12 \pm 0.43 0.48-4.28
	last 3 days	11 (66-220) 1.90 \pm 0.44 0.48-5.51	last 3 days	9 (46-133) 2.03 \pm 0.56 0.11-5.77

TABLE 2
CONTINUED

Period	Sample interval (days)	Songs/min all contexts N* $\bar{x} \pm SE$ range \bar{x}^b	Sample interval	Songs/min male-alone-distant N $\bar{x} \pm SE$ range \bar{x}
Fledgling	first week	11 (70-340) 1.99 \pm 0.47 0.08-4.45	—	—
	to 4th week	6 (195-319) 1.29 \pm 0.55 0-3.43	—	—

* N is individuals sampled.

^b Range \bar{x} is the range in means of individuals in songs/min.

^c The range in total minutes recorded.

(1.43 songs/min, N = 9, samples for individuals ranged from 50-179 min) and was found to be significantly lower ($P < 0.01$) than the previous two contexts.

There occurred a significant increase ($P < 0.05$) in song output from the early pre-nest-building period to the first two days of the nest-building period. In part, an increase in song activity is expected in the nest-building period as males spend more time in contexts where they sing actively; 73.2% (N = 1538 min, N = 7 individuals) of the males' time was spent alone and away from the nest or near the nest. Song output decreased slightly during the nest-building period then increased during the first 3 days of the incubation period, however, differences were not significant (largest $t = 2.059$, $P > 0.10$). In the context male-alone-distant there occurred a significant increase ($P < 0.05$) in song rate between the first half of the nest-building period and the first 3 days of the incubation period. The increase was not associated with any obvious changes in the number or intensity of territorial interactions. The decrease in overall output during the nest-building period is likely due to changes in activity patterns. Males spend increasingly more time with the female during this period and, because the pair is away from the nest (26.9%, N = 1538 min) more than they are near it (9.1%, N = 1538 min), a decrease in male song output is to be expected. Song output at the beginning of the incubation period is high then because males spend all their time in contexts in which they sing actively (e.g., on the nest, patrolling the territory). At the beginning of the incubation period males tended to sing continually while on the nest.

There occurred a gradual and significant decrease ($P < 0.01$) in both overall song output and song output in the context male-alone-distant from the beginning of the incubation period to the end of the nestling period. The change in song rate was not attributable to any obvious change in the activity patterns of males, which remained relatively constant from day to day.

Breeding season and patterning of song.—To determine if a change in delivery of song occurred when the amount of singing changed, data on song activity were gathered when output was high (early incubation period) and low (early nestling period) for two contexts: male-alone-distant and male-on-the-nest (Table 3). A significant decrease ($P < 0.01$) occurred in both song and singing rates and a significant increase ($P < 0.05$) in the time spent silent from the early incubation period to the early nestling period for both contexts. The mean cadence values were not significantly different. The results may be due to differences in the continuity of song when the amount of singing changes. At low output levels song tends to be given in short bouts or sporadically. Song becomes less spontaneous and tends to be given only in response to specific stimuli such as during movements near the nest, at nest relief, and during interactions with neighboring males. At low output there occurs a greater number of minutes in which only one or two songs are recorded than when output is high. This would result in a lower singing rate, but would not necessarily affect cadence values.

Song activity and behavior.—During the nest-building period males spent 36% ($N = 1538$ min, $N = 7$ individuals) of their time accompanying their females to and from the nest. During this time the female gathers nesting material and constructs the nest. When the pair is together and away from the nest, the male is silent or sings infrequently. However, when approaching the nest the male sings at an increased rate and constantly. The effect of nest-centered song activity is apparent during courtship. A female mostly gives courtship vocalizations (see Methods) but also solicits by giving wing-quivers (for description see Barlow and Rice 1977), an apparent and immediate response to male song. However, this behavior by females is largely restricted to the vicinity of the nest (Howes-Jones 1982). Most courtship vocalizations (74%, $N = 50$) and wing-quivers (97%, $N = 104$) occurred within 10 m of the nest. Proximity to the nest appears necessary for female courtship behavior to be exhibited. Closeness to the nest seems especially important for the stimulation of wing-quivers. The female quivers her wings near the nest even when the male is not present or singing. Away from the nest pairs rarely engaged in courtship activity, however, when they approached the nest courtship activity commenced. Almost all copulatory attempts (48 of 50) were observed within 10 m of the nest.

TABLE 3
CHANGES IN SONG ACTIVITY WHEN SONG OUTPUT IS HIGH AND LOW

Song Variables	Context			
	Male-alone-distant		Male-on-the-nest	
	Sample period		Sample period	
	Incubation	Nestling	Incubation	Nestling
	N $\bar{x} \pm SE$	N $\bar{x} \pm SE$	N $\bar{x} \pm SE$	N $\bar{x} \pm SE$
Song rate (includes 0 songs/min)	10	10***	10	10***
	5.08 \pm 0.56	2.19 \pm 0.41	3.20 \pm 0.50	0.89 \pm 0.24
Singing rate (excludes 0 songs/min)	10	10***	10	10**
	6.08 \pm 0.36	3.94 \pm 0.30	3.64 \pm 0.41	2.00 \pm 0.31
Time spent silent (%)	10	10*	10	10***
	16.24 \pm 7.12	48.37 \pm 8.84	16.49 \pm 6.30	64.90 \pm 8.03
Cadence (sec)	10	10 ^{NS}	10	9 ^{NS}
	9.27 \pm 0.40	10.37 \pm 0.44	14.33 \pm 1.00	14.76 \pm 1.23

Statistical comparisons (*t*-test) are between periods for each context. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ NS = not significant.

During the incubation and nestling periods nest-centered song activity was evident during exchanges by adults involved in incubation, brooding, and feeding of young. In both periods males sang on 94.4% ($N = 820$) of their trips to the nest and on 65.1% ($N = 690$) of their departures from the nest. When a male approaches the nest his song appears to be a cue to the female to fly from the nest. Near the end of the incubation period some males sang only when flying to the nest. In response, the female almost always flew off the nest.

All male Warbling Vireos which I observed sang while sitting on the nest. The regular and moderately paced song given by incubating or brooding males is distinctive and to the experienced observer indicates the bird's activity. Generally, when the male is on the nest the female initiates an exchange of positions by approaching the nest and calling. At this point the male flies off the nest. Less often the male may initiate an exchange of position. Two methods are used. In the first case the male flies off the nest when the female is absent and silent. After a short delay the female flies to the nest. In the second case, if a male has been sitting on the nest for a long period he may start to sing faster, at which point the previously distant female may then fly to the nest. Males sitting on the nest sometimes increase the tempo of song in response to an approaching female.

DISCUSSION

Smith (1977) suggests that animals maximize their limited 'message space' by using contextual sources of information which increase the functional breadth or range of the signal. In the Warbling Vireo, song rate, cadence, and output changed with the proximity of the male to the nest, to the female, and with the stage of the breeding season. Changes in song activity appear to function in a variety of ways to help integrate the social activities of the pair.

During the nest-building period nest-centered singing appears important in the integration of sexual activities. Both proximity to the nest and male song appear necessary to evoke courtship behavior by the female. If both factors are important, then nest-centered song is advantageous because it promotes maximal stimulation of the female in a locale where she is already primed for activity. In this context, song likely exerts a tonic or priming effect on the female (Schleidt 1973, Smith 1977:234). Reduction in singing, which occurs when the pair is together and away from the nest, is also advantageous because it minimizes stimulation of the female in an area where copulation is not likely to occur and also may reduce interference from neighboring males.

One of the functions accredited to passerine song as a courtship signal is in the sexual stimulation of the female and the synchronization of courtship behavior (Brockway 1965, 1969; Armstrong 1973:156-160; Hinde and Steel 1976; Kroodsma 1976; Miller 1979). The role that the amount of song plays in courtship in *V. gilvus* is not clear. In many passerines song output peaks several days before egg-laying at a time corresponding to ovulation (Catchpole 1973, 1982; Slagsvold 1977). However, this relationship may not be a general one, as Armstrong (1973) lists many species in which peak singing does not coincide with a time several days before egg-laying. In the Warbling Vireo song output peaked at the start of the incubation period. Although total song output (all contexts) is likely important in the stimulation of the female, it is possible that singing in the appropriate context is also important. A continuous and high rate of song near the nest during the nest-building period is likely the important factor in the Warbling Vireo. Brockway (1969) found in Budgerigars (*Melopsittacus undulatus*) that only a certain quantity of the appropriate vocal stimuli was important in stimulating the female and that a further increase in quantity had no effect.

At the start of incubation, nest-centered song acquired the different function of coordinating movements of the pair to and from the nest. The giving of song on approaches to the nest signals the male's presence and probable intention to sit on eggs and acts as a cue for the female to

fly off the nest. In this context, song activity has a more discreet effect or is informative (Schleidt 1973, Smith 1977:234).

Singing by male Warbling Vireos on the nest has been noted by others (Miller 1902, Rust 1920, Sutton 1949, Bent 1950). The contrast in cadence, rate, and direction of song, which occurs when the male is on then flies off the nest, allows the female to ascertain when the male is on the nest and when she should fly to the nest. Warbling Vireos can and do use a variety of call notes to maintain contact and synchronize movements at the nest (Howes-Jones 1982), which suggests that there might be other reasons why males sing on the nest. Singing from the nest may be tied to the fact that Warbling Vireos are prodigious singers and have complex songs (Hartshorne 1956, Howes-Jones 1982). A cessation of song on the nest would create a regular and obvious on-off pattern in song activity which might alert potential nest predators. Regular vocal contact is essential to the relationship between mates (Howes-Jones 1982). Consistency in the output of song may also be tied to the maintenance of the territory.

Reduction of song during pair formation is characteristic of many passerines and has often been used as evidence to indicate that active singing attracts females (Armstrong 1973:152, Catchpole 1982). In the Warbling Vireo the reduction in overall song output at pairing was due mostly to a change in activity patterns (i.e., female presence seemingly causes a reduction in male song). The song rate in the pre-pair period was slightly lower than the song rate in the comparable context (male-alone-distant) in the pre-nest-building period. This difference does not preclude the fact that a high song rate may attract females. It does indicate that the effect of female presence on song activity is context specific. That a high rate and output of song may attract mates is also indicated by the observation that the song output of a male whose female disappeared during the incubation period increased substantially. For two males that remained mated after their nests were destroyed, however, song output remained unchanged. When the male and female are together prior to nest-building, song activity is unique (variable cadence, sporadic output, large amount of time spent silent) and as such may convey that the male has a mate.

In this study part of the variation in song output during the season was ascribed to changes in the activity patterns of birds. The fact that song activity can change with context suggests that any interpretation of general or seasonal changes in song output requires the examination of both context related factors and changes in activity patterns. A decline in singing during incubation is typical of other birds and has generally been ascribed to a reduction of androgen levels and to the appearance of the

young (Davis 1958, Lehrman 1959, Andrew 1969, Lofts and Murton 1975, Nottebohm 1975).

Differences in cadence among species have been described (Reynard 1963), however, changes in cadence among contexts within a species are not well understood. In other passerines cadence has been found to increase when males sang with neighbors (Heckenlively 1976), to be regular, or to increase with a decrease in output (Davis 1958). The relevance of the patterning of songs over an extended period of time (i.e., bouts) has also received scant attention (for exception see Thompson 1972). The general problem of temporal patterning in song, its relationship to context, and encoded message requires further research.

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SUMMARY

The song activity of Warbling Vireos (*Vireo gilvus*) in southern Ontario was quantified using the variables of song rate, cadence, and time spent silent. Song activity changed substantially with context (six defined) and with season. Contexts were defined in terms of the proximity of the male to the female and to the nest. In the immediate proximity of females, males are silent or sing sporadically except when engaged in a song duel with another male or when near the nest. In close proximity to the nest, song tends to be continuous and has a short cadence. Song delivered on the nest has a long and regular cadence. Males appear to sing in bouts only when they are alone, away from the nest, and are patrolling their territories. In part, changes in song output with different stages of the breeding cycle were due to changes in activity patterns as the result of the context dependency of song rate and output. Gradual changes in song activity occurred during the breeding cycle. Changes in song activity were related to: establishing contact with a potential mate; integrating courtship behavior so that it occurs only in the vicinity of the nest; as a means for monitoring a bird's activity and location; and in coordinating movements of birds to and from the nest.

LITERATURE CITED

- ANDREW, R. J. 1969. The effects of testosterone on avian vocalization. Pp. 97-130 in *Bird vocalizations* (R. A. Hinde, ed.). Cambridge Univ. Press, Cambridge, England.
- ARMSTRONG, E. A. 1973. *A study of bird song*, 2nd ed. Dover Publ., New York, New York.
- BARLOW, J. C. AND J. C. RICE. 1977. Aspects of the comparative behaviour of Red-eyed and Philadelphia vireos. *Can. J. Zool.* 55:528-542.
- BENT, A. C. 1950. *Life histories of North American wagtails, shrikes, vireos and their allies*. Bull. U.S. Natl. Mus. 197.
- BROCKWAY, B. F. 1965. Stimulation of ovarian development and egg laying by male courtship vocalization in budgerigars (*Melopsittacus undulatus*). *Anim. Behav.* 13:575-578.

- . 1969. Role of budgerigar vocalizations in the integration of breeding behaviour. Pp. 131–158 in *Bird vocalizations* (R. A. Hinde, ed.). Cambridge Univ. Press, Cambridge, England.
- CATCHPOLE, C. K. 1973. The functions of advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). *Behaviour* 46:300–320.
- . 1982. The evolution of bird sounds in relation to mating and spacing behavior. Pp. 297–319 in *Acoustic communication in birds*, Vol. 1 (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, New York.
- DAVIS, J. 1958. Singing behavior and the gonad cycle of the Rufous-sided Towhee. *Condor* 60:308–336.
- DAWKINS, R. 1976. Hierarchical organization: a candidate principle for ethology. Pp. 7–54 in *Growing points in ethology* (P. P. G. Bateson and R. A. Hinde, eds.). Cambridge Univ. Press, Cambridge, England.
- EMLEN, S. T. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41:130–171.
- FALLS, J. B. 1963. Properties of bird song eliciting responses from territorial males. *Proc. XIII Int. Ornithol. Congr., Ithaca, New York* 1:259–271.
- . 1969. Function of territorial song in the White-throated Sparrow. Pp. 207–232 in *Bird vocalizations* (R. A. Hinde, ed.). Cambridge Univ. Press, Cambridge, England.
- HARTSHORNE, C. 1956. The monotony-threshold in singing birds. *Auk* 73:176–192.
- HECKENLIVELY, D. B. 1976. Variation in cadence of Field Sparrow songs. *Wilson Bull.* 88: 588–602.
- HINDE, R. A. 1958. Alternative motor patterns in Chaffinch song. *Anim. Behav.* 6:211–218.
- AND E. STEEL. 1976. The effect of male song on an estrogen-dependent behaviour pattern in the female Canary (*Serinus canarius*). *Horm. Behav.* 7:293–304.
- HOWES-JONES, D. 1982. The structure of an avian vocal communication system. Ph.D. diss., Univ. of Toronto, Toronto, Ontario.
- KROODSMA, D. E. 1975. Song patterning in the Rock Wren. *Condor* 77:294–303.
- . 1976. Reproductive development in a female songbird: differential stimulation of quality of male song. *Science* 92:574–575.
- . 1977. Correlates of song organization among North American wrens. *Am. Nat.* 111:995–1008.
- LEHRMAN, D. S. 1959. Hormonal responses to external stimuli in birds. *Ibis* 101:478–496.
- LEIN, M. R. 1978. Song variation in a population of Chestnut-sided Warblers: its nature and suggested significance. *Can. J. Zool.* 56:1266–1283.
- LOFTS, B. AND R. K. MURTON. 1975. Reproduction in birds. Pp. 1–107 in *Avian biology*, Vol. III (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.
- MARLER, P. 1956. The voice of the Chaffinch and its function as a language. *Ibis* 98:231–261.
- MESAROVIC, M. D. AND D. MACKO. 1969. Foundations for a scientific theory of hierarchical systems. Pp. 29–50 in *Hierarchical structures* (L. L. Whyte, A. G. Wilson, and D. Wilson, eds.). Elsevier Publ. Co., New York, New York.
- MILLER, D. B. 1979. The acoustic basis of mate recognition by female Zebra Finches (*Taeniopygia guttata*). *Anim. Behav.* 74:376–380.
- MILLER, M. M. 1902. The Warbling Vireo, a nest singer. *Bird Lore* 4:161–162.
- MORSE, D. H. 1967. The contexts of songs in Black-throated Green and Blackburnian warblers. *Wilson Bull.* 79:64–74.
- NOTTEBOHM, F. 1975. Vocal behavior in birds. Pp. 287–332 in *Avian biology* vol. V (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

- POLANYI, M. 1968. Life's irreducible structure. *Science* 166:1302-1312.
- REYNARD, G. B. 1963. The cadence of bird song. *Living Bird* 2:139-148.
- RUST, H. J. 1920. The home life of a western Warbling Vireo. *Condor* 22:85-94.
- SCHLEIDT, W. M. 1973. Tonic communication: continual effects of discrete signs in animal communication systems. *J. Theor. Biol.* 42:359-386.
- SIMON, H. J. 1962. The architecture of complexity. *Proc. Am. Phil. Soc.* 106:469-482.
- SLAGSVOLD, T. 1977. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. *Ornis Scand.* 8:197-222.
- SMITH, W. J. 1965. Message, meaning, and context in ethology. *Am. Nat.* 99:405-409.
- . 1968. Message—meaning analysis. Pp. 44-66 in *Animal communication* (T. A. Sebeok, ed.). Indiana Univ. Press, Bloomington, Indiana.
- . 1977. *The behaviour of communicating*. Cambridge Univ. Press, Cambridge, England.
- , J. PAWLKIEWICZ, AND S. T. SMITH. 1978. Kinds of activities correlated with singing patterns of the Yellow-throated Vireo. *Anim. Behav.* 26:862-884.
- SOKAL, R. R. AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Co., San Francisco, California.
- SUTTON, G. M. 1949. Studies of nesting birds of the Edwin S. George Reserve. Part I. The Vireos. *Misc. Publ. Mus. Zool., Univ. Mich.*, No. 74.
- THOMPSON, W. L. 1972. Singing behaviour of the Indigo Bunting (*Passerina cyanea*). *Z. Tierpsychol.* 31:39-59.
- THORPE, W. H. 1961. *Bird song. The biology of vocal communication and expression in birds*. Cambridge Univ. Press, Cambridge, England.

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ERRATA

In D. A. Boag's review of "The grouse of the world" by P. A. Johnsgard (*Wilson Bull.* 96:337-338, 1984), the genus name of *Dendragapus* is misspelled on page 338. Also, the penultimate sentence should read "... the Spruce and Sharp-winged grouse closer to the Blue Grouse . . ."